

Seasonal Occurrence and Aggregation Behavior of the Sea Urchin *Astropyga pulvinata* (Echinodermata: Echinoidea) in Bahía Culebra, Costa Rica¹

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Abstract: Between October 2003 and July 2005, aggregation behavior of the sea urchin *Astropyga pulvinata* Lamarck was studied in Bahía Culebra, Costa Rica. This sea urchin forms aggregations during part of the year and then disappears. I quantified the number of individuals present in a defined area each month, their aggregation behavior between day and night, and their size. Also, temperature and nutrient concentrations of the water were sampled. There were significantly more individuals in aggregations during the colder, upwelling season (December to April). Aggregations consisted of adult individuals that exploit food during the upwelling season. Moreover, these aggregations were used as a refuge by several fish species of high commercial value for the aquarium trade. These sea urchin populations could suffer as extraction of ornamental fishes and urchins increases. Their abundance and behavior should continue to be monitored as an indication of the ecological health of the community.

DIADEMATID SEA urchins are among the most important and familiar inhabitants of tropical and subtropical waters (Hyman 1955). Their ability to occupy different niches is an important factor in their success; they live on coral reefs, mangrove roots, sea grasses, and sand flats. Moreover, their success is linked to their generalist diet and their efficiency in use of the resources available. They are found in caves, overhangs, and crevices that provide protection against predators, and they are more abundant in zones protected from strong waves. For that reason, if wave stress increases, or if predators or competitors are present, diadematids tend to aggregate. They play an important role on

reef areas due to their substantial effects on the biomass, structure, and distribution of seaweeds, as well as on coral composition and reef geomorphology because they are bioeroders (see review by Birkeland 1989).

In the eastern tropical Pacific there are five diadematid species in four genera: *Astropyga*, *Centrostephanus*, *Echinobrix*, and *Diadema*. The last genus has received more attention in the eastern Pacific due to the important role of *Diadema mexicanum* as a reef bioeroder and controller of seaweed populations (Glynn 1988, Guzmán 1988, Fischer 1990, Guzmán and Cortés 1992, 2007, Herrera-Escalante et al. 2005). Also, its reproductive cycle and population structure (Lessios 1981, Espino-Barr et al. 1996) have been studied, as well as its phylogeographic relationships (Lessios et al. 2001). With respect to *Centrostephanus coronatus*, its bioerosional impact (Toro-Farmer et al. 2004), role in controlling algae (Vance 1979), and reproductive cycle (Kennedy and Pearse 1975) have been studied. But there are very few papers on *Echinobrix* and *Astropyga* in the eastern Pacific.

Members of the genus *Astropyga* are among the most conspicuous diadematids, with a series of iridescent blue spots on the test, thin spines, and a large, flexible, and very low test (Mortensen 1940, Caso 1978).

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Astropyga is found in tropical and subtropical waters of the Caribbean, Indo-Pacific, and eastern Pacific and includes three species (Mortensen 1940): *A. magnifica*, *A. radiata*, and *A. pulvinata*. *Astropyga pulvinata* Lamarck has been reported from the Gulf of California (Solís-Marín et al. 2005), El Salvador (Barraza and Hasbún 2005), Panamá (Lessios 2005), Colombia (Neira and Cantera 2005), the Galápagos Islands (Hickman 1998), and Lobos de Afuera Island in Perú (Hooker et al. 2005). It occurs on sand, rock, or muddy substrates (Clark 1940, Caso 1978, Hickman 1998) between 2 and 95 m deep (Clark 1948, Hickman 1998; C. Fernández, pers. comm.). It possesses a flat test with triangular white areas on the interambulacral zones (Mortensen 1940) and a maximum test diameter of 120 mm (Brusca 1980). This species eats any kind of bottom material with foraminifera and small gastropods (Mortensen 1940, De Ridder and Lawrence 1982). In several sections of the American coast, large aggregations of this sea urchin have been observed, generally during the upwelling season, but they later disappear (Hickman 1998, Hooker et al. 2005, Lessios 2005).

Diadematid aggregations have been observed in many places around the world, like the Great Barrier Reef of Australia, in Japan, Suez, in the Caribbean, and in the eastern Pacific (see references in Pearse and Arch [1969]). In Huatulco Bay, on the Pacific coast of Mexico, aggregations of *Diadema mexicanum* composed of hundreds of individuals caused intense grazing on a dead reef of *Pocillopora* (Glynn and Leyte-Morales 1997). Aggregations of *Astropyga pulvinata* have been observed in several localities in the eastern Pacific: in the Galápagos Islands (Albany Island) aggregations of two to ~300 individuals in depths around 12 m appear in February and disappear in November (Hickman 1998). Aggregations have been observed sporadically during some times of the year on Cocos Island, and then they disappear suddenly (N. Gersinich, pers. comm.). In Panamá, during the upwelling season, they can be found in great concentrations in the Gulf of Panamá (Changame Island), over sand at approximately 10 m depth (Lessios 2005). At Lobos

de Afuera Island, Perú, they formed numerous aggregations on rocky reef between 0 and 5 m deep in June 1999 (Hooker et al. 2005).

The objective of this work is to describe basic ecological characteristics of *Astropyga pulvinata* in Bahía Culebra, on the northern Pacific coast of Costa Rica. Abundance, density, degree of aggregation, and population structure are described as well as their relation to several physicochemical parameters, with the goal of determining the spatial and temporal extent of aggregations and which parameters might control them.

MATERIALS AND METHODS

The study took place between October 2003 and July 2005, at Punta Flor (10° 37' 26.80" N, 85° 40' 45.4" W) (Figure 1) in the inner part of Bahía Culebra on the north Pacific coast of Costa Rica. This bay is subjected to a seasonal upwelling of cool, rich waters between December and April (Brenes et al. 1990, Jiménez 2001). It consists of a series of inlets, beaches, sea cliffs, and estuaries with economically important marine resources (Jiménez 2001). It is a zone rich in coral reefs, with approximately 16 species of reef-building corals, and live coral cover of 44% (Jiménez 2001). Punta Flor is located on the inner part of the bay, in the north section. It is a zone surrounded by sea cliffs with scarce vegetation, a narrow intertidal zone, and a sea bottom composed mainly of coarse and medium sand (C. Fernández, unpubl. data).

Biological Variables

Astropyga pulvinata is a common sea urchin in Bahía Culebra that in some periods of the year forms aggregations (two or more individuals close together, touching at least by their spines) (Figure 2). With the goal of understanding this behavior, the dynamics of the aggregations were studied between October 2003 and July 2005 in Punta Flor (Figure 1). The monthly density of the sea urchin and the aggregation behavior between day and night were determined by measuring the distance between individuals. To determine

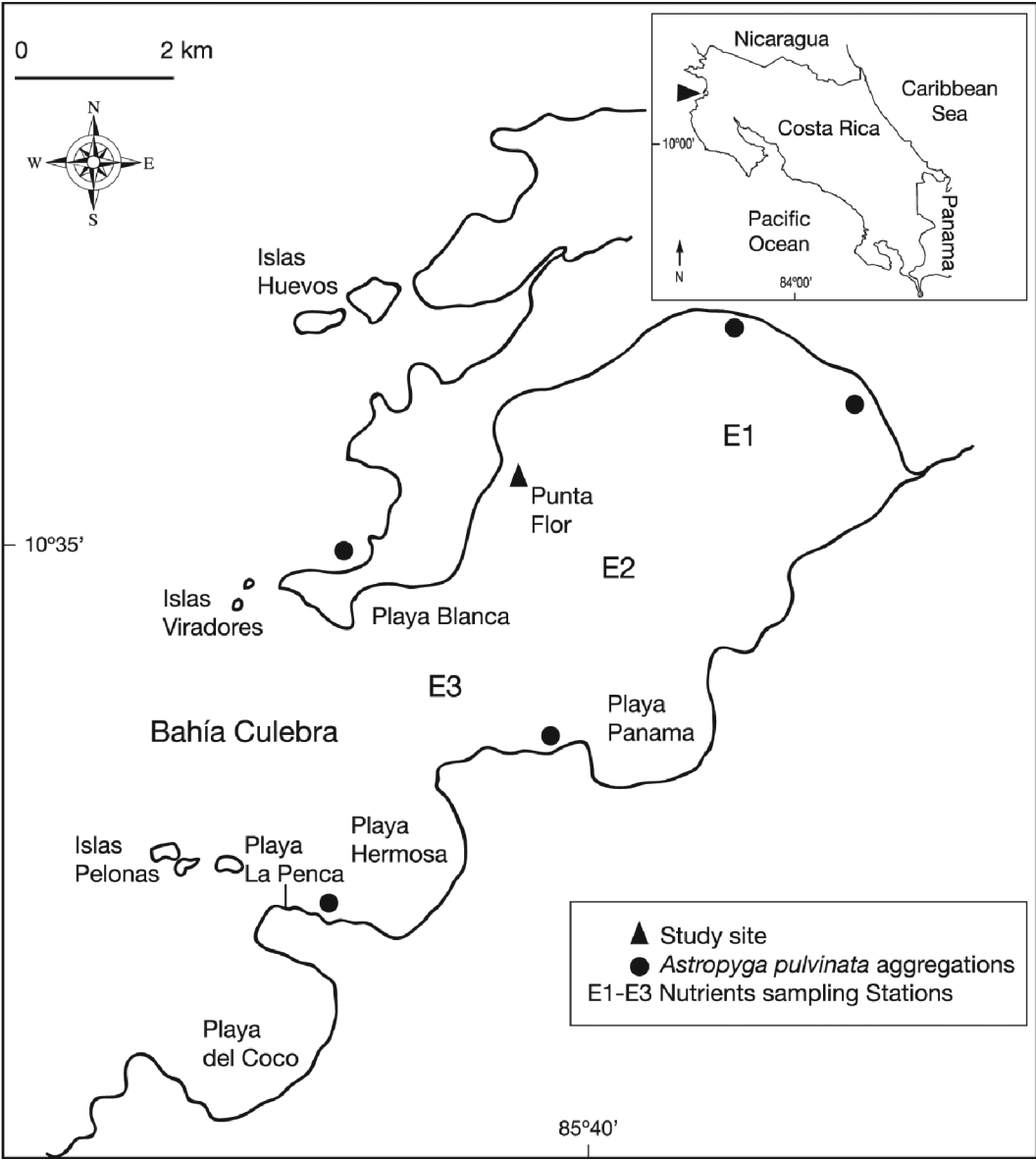


FIGURE 1. Punta Flor location in Bahía Culebra, sites where *Astropyga pulvinata* aggregations occur, and nutrient sampling stations inside the bay.

abundance, all individuals of the sea urchin were counted monthly in an area of 3,125 m² (125 m long by 25 m wide). The area was covered in a zigzag manner from around 2 m depth down to 8–10 m (approximately 25 m from the coastline), counting all the aggrega-

tions and the number of sea urchins per aggregation. The sampling always took place between 0800 and 1000 hours. Between November 2003 and February 2004 night dives were done, between 1830 and 2000 hours, to observe the nocturnal aggregation behavior.

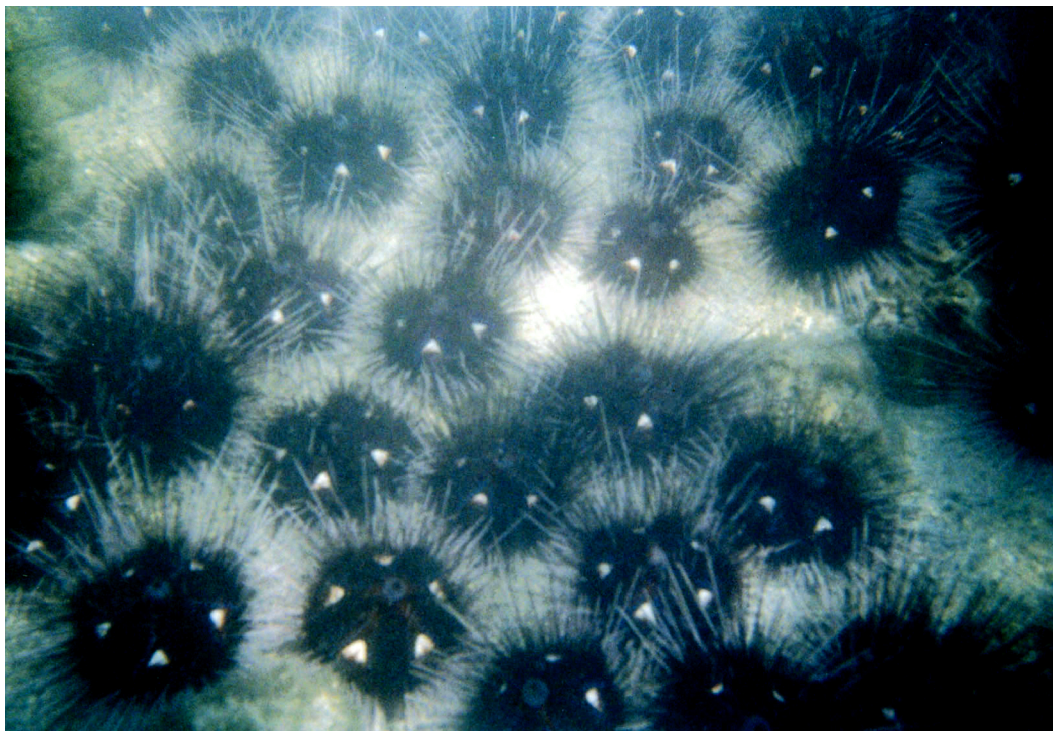


FIGURE 2. *Astropyga pulvinata* adult aggregation at Punta Flor, Bahía Culebra.

The diameter of the test was measured, between November 2003 and September 2004 with a caliper, to define population structure over time. Ten individuals were measured per aggregation, so the total number measured depended on the number of aggregations during the sampling dive. This procedure followed the same zigzag pattern, always measuring and counting the urchins in the same direction to avoid counting the same individuals twice.

Finally, between January and February 2004, the distance between individuals was measured with a metric tape from the border of the test of the urchin to the nearest neighbor test, during the day and night, to determine if there is a higher or lower degree of aggregation depending on the time of the day. We counted a minimum of 50 individuals per dive. The results are presented as averages \pm the standard deviation.

Nonparametric Kruskal-Wallis tests were

done to determine if there were differences between: (a) the total number of individuals per month (or density) and the season of the year (upwelling and nonupwelling); (b) the distance between individuals and the time of day; (c) the number of aggregations and the time of day; (d) the total number of individuals per sampling and the time of day; and (e) the average of individuals per aggregation and the time of day.

Physicochemical Variables

As part of a Centro de Investigación en Ciencias del Mar y Limnología (CIMAR) monitoring program, seawater temperature was recorded every 30 min with a data logger (StowAway) located at 6 m depth on the Playa Blanca reef (Figure 1). The concentration of phosphate (PO_4^{3-}) at three stations in the bay (E1, E2, E3) (Figure 1) was determined as a proxy of the productivity of the environment.

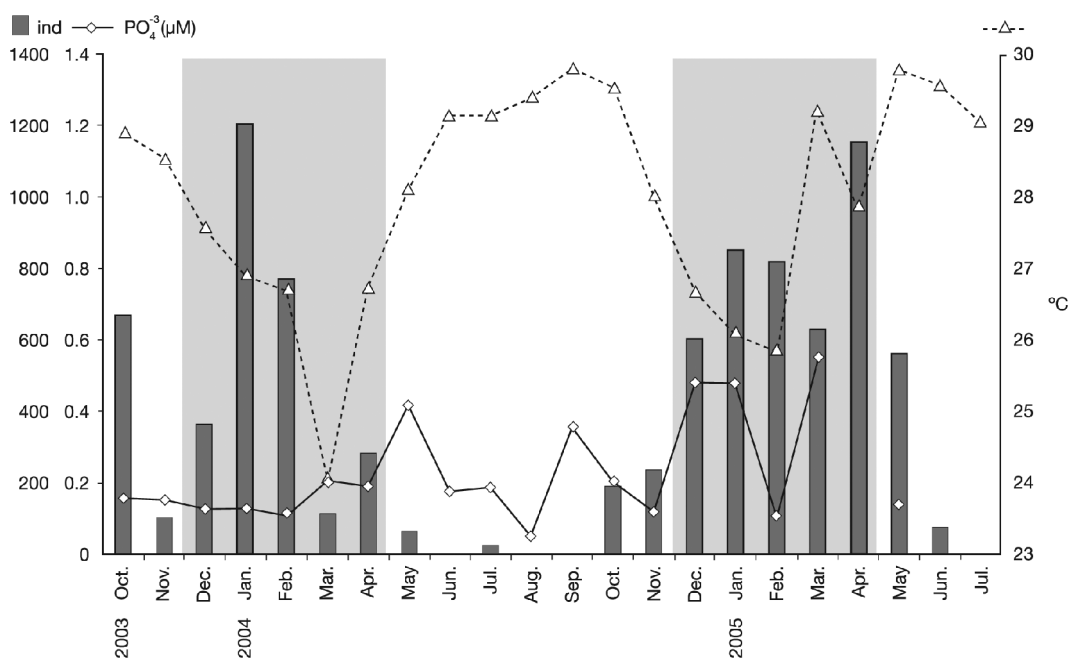


FIGURE 3. Total individuals of *Astropyga pulvinata* observed per month (columns), monthly average seawater temperature ($^{\circ}\text{C}$, open triangles), and average phosphorus concentration (μM , open diamonds) at Punta Flor, Bahía Culebra. No phosphorus determinations were available for April, June, and July 2005. The upwelling season is indicated by gray shading.

Every month at each station, 1 liter of surface water was sampled and later analyzed following the procedures of Strickland and Parsons (1972) using a spectrophotometer (Shimadzu UV-160A).

Linear regressions between monthly average temperature and nutrient concentrations, and total numbers of individuals per month were done. All the data were transformed with the function $\log_{10}(x + 1)$ and analyzed with the programs Systat 8.0 (Systat Software 1998) and JMPin 4.0 (SAS Institute 2001).

RESULTS

Physicochemical Variables

During the study period, the average sea temperature was $27.8 \pm 1.57^{\circ}\text{C}$, being maximal in September 2004 (29.8°C) and minimal in March 2004 (24.1°C), corresponding with the rainy and the dry (upwelling) season, respectively (Figure 3). The average phospho-

rus concentration was $0.23 \pm 0.15 \mu\text{M}$, with a maximum value of $0.56 \mu\text{M}$ in March 2005 and a minimum of $0.05 \mu\text{M}$ in August 2004. Phosphate followed a pattern opposite to that of temperature, with high values during the dry season (upwelling) (Figure 3).

Biological Variables

Astropyga pulvinata was more abundant during the upwelling season and almost absent in the nonupwelling season (Figure 3). An average of 679 ± 356 individuals per month was calculated for the upwelling season and 159 ± 226 individuals per month for the nonupwelling season. It was most abundant in January 2004 (1,203 individuals) and absent in June, August, and September 2004 (Figure 3). A significant difference was detected among seasons between the numbers of individuals (dry versus rainy season) ($\text{KW} = 10.0$, $P < .01$, $n = 22$). No relationship was detected between the concentrations of phos-

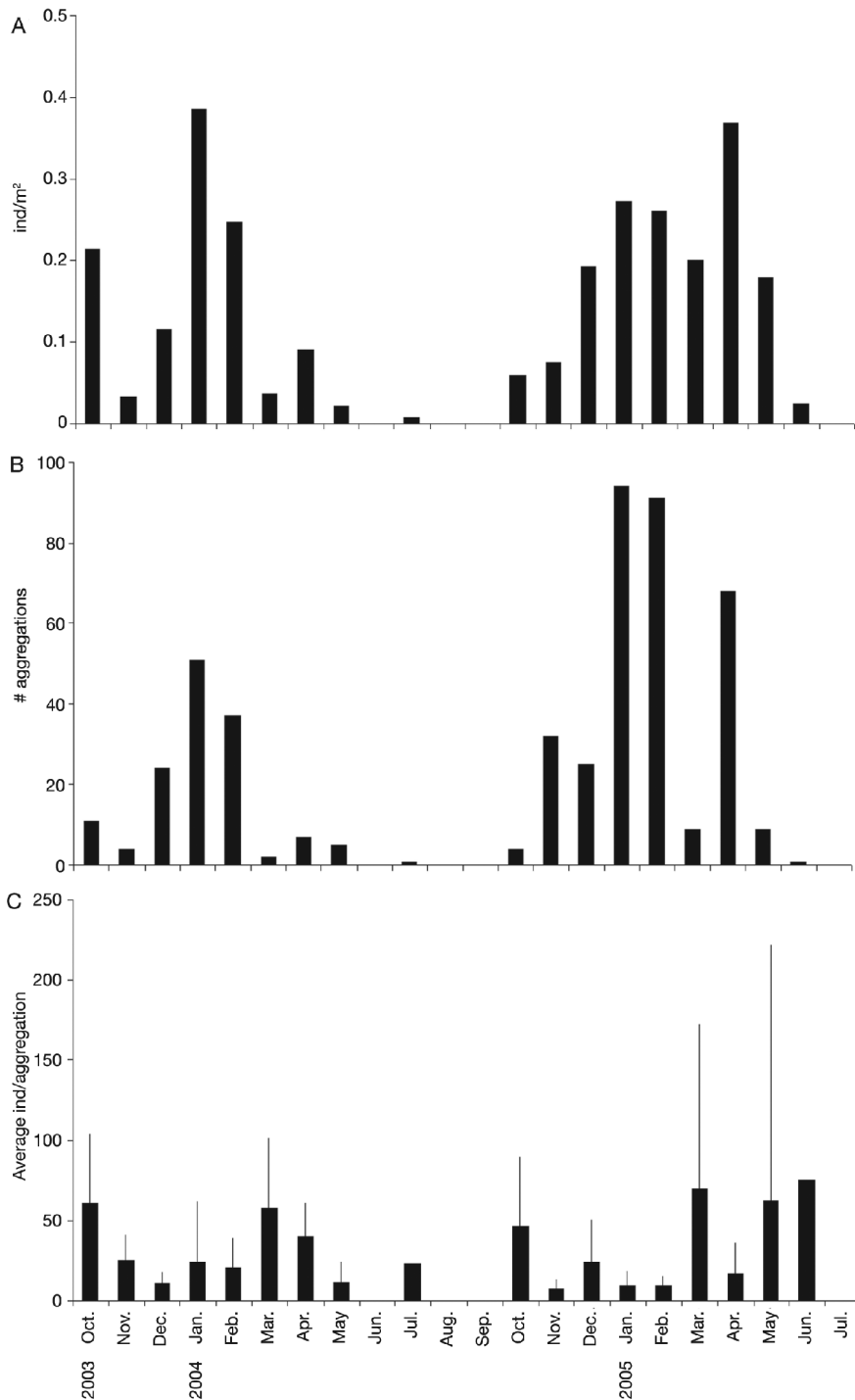


FIGURE 4. (A) Density (individuals per square meter), (B) number of aggregations, and (C) average and standard deviation of individuals per aggregation of *Astropyga pulvinata* at Punta Flor, Bahía Culebra, between October 2003 and October 2005.

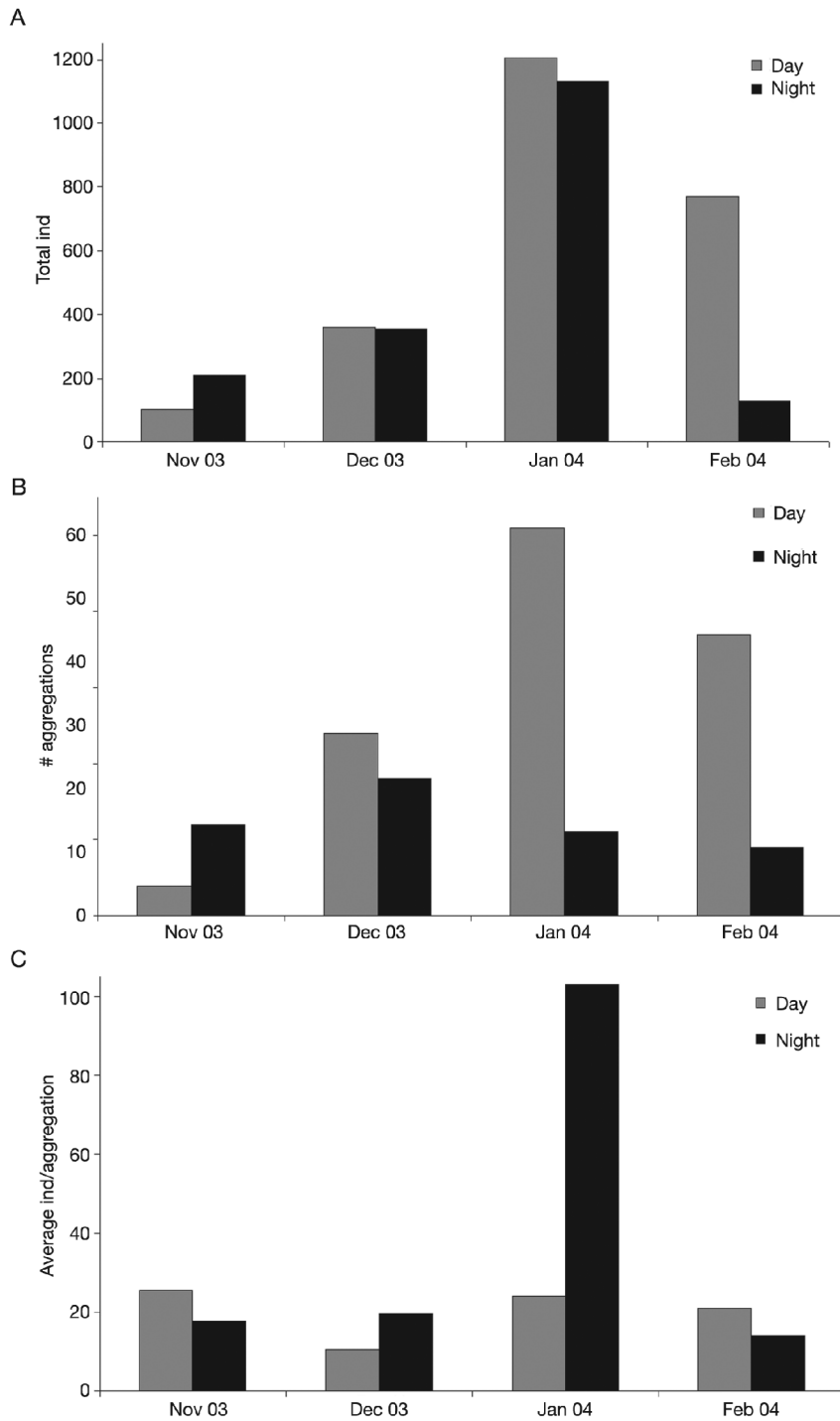


FIGURE 5. Comparison of aggregations of *Astropyga pulvinata* at Punta Flor, Bahía Culebra, between day and night from November 2003 to February 2004. (A) Total individuals, (B) number of aggregations, and (C) average number of individuals per aggregation.

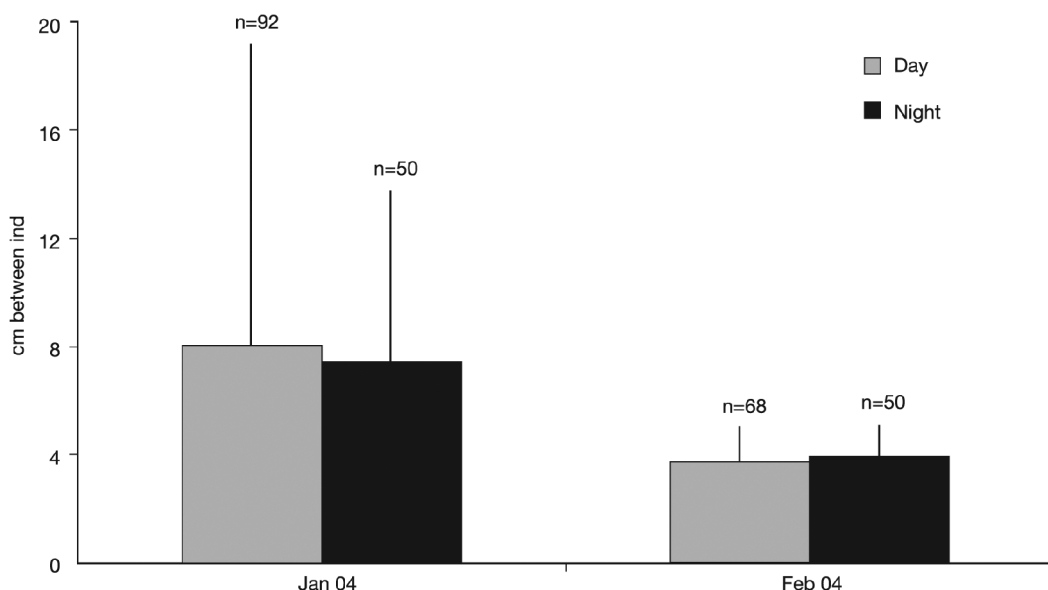


FIGURE 6. Average distance (centimeters) and standard deviation between individuals of *Astropyga pulvinata* in day and night aggregations at Punta Flor, Bahía Culebra, January and February 2004.

phate and the quantity of individuals per month, but there was a significant negative relationship with temperature ($R^2 = 0.21$, $P < .05$).

The average density was 0.13 ± 0.12 individuals per square meter, 0.2 ± 0.1 individuals per square meter for the upwelling season, and 0.1 ± 0.1 individuals per square meter for the nonupwelling season, with two maximal values of 0.38 and 0.37 individuals per square meter for January 2004 and April 2005, respectively (Figure 4A). The highest numbers of aggregations between 0800 and 1000 hours were observed in January, February, and April 2004 with 94, 91, and 68 aggregations per month, respectively (Figure 4B), and an average of 21.6 ± 29.3 aggregations per month, 40.8 ± 34 aggregations per month for the upwelling season, and 5.6 ± 9.1 aggregations per month for the nonupwelling season. On average each aggregation had 26.9 ± 24.5 individuals. June 2005 (a nonupwelling month) was the month with the highest number of individuals per aggregation (75), followed by March 2005 (69.7) (Figure 4C). In June 2005 there was only

one aggregation, and in March 2005 there were nine aggregations with a total of 559 individuals. January 2004, with 24 individuals per aggregation, was the month with the highest number of individuals (1,203).

There was no statistical difference between the average number of individuals during the day (610 ± 482) and during the night (457 ± 460) ($P = .56$). There were also no statistical differences between average numbers of aggregations during the day (29.0 ± 20) and at night (12.5 ± 3.9), or between average number of individuals per aggregation in the night (38.6 ± 43.0) and in the day (20.2 ± 6.8), ($P = .24$, $P = 0.73$, respectively) (Figure 5). Also, no significant difference was found in the distance between individuals in the day (5.9 ± 3.1 cm) and the night (5.7 ± 2.5 cm) (KW = 9,045, $P = .08$, $n = 261$) (Figure 6).

Most individuals had a test diameter between 70 and 120 mm (101.3 ± 3.6 mm) (Figure 7). The predominant size was between 90 and 100 mm, which corresponds to adult size. The ~70 mm size corresponds to large juveniles, and they had a different color

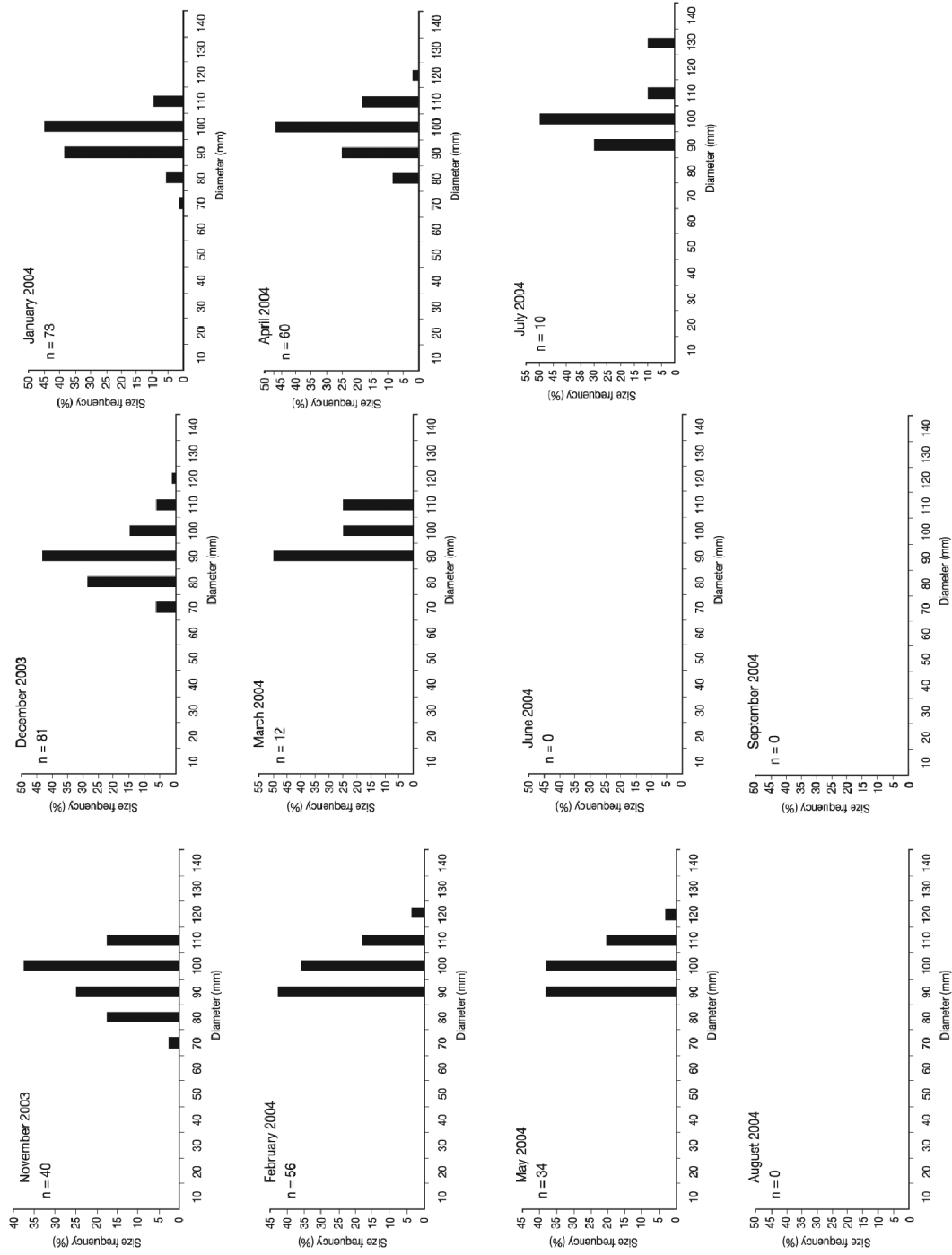


FIGURE 7. Monthly size (diameter of the test in millimeters) frequency (%) distribution of *Astropyga pulvinata* at Punta Flor, Bahía Culebra, between November 2003 and September 2004. For June, August, and September 2004 no individuals were recorded in the area.

pattern than the adults. The sizes reported herein are within the range reported for the region (15–117 mm) (Clark 1923, 1940, 1948, Caso 1961, 1978, Lessios 1990). Clark (1948) pointed out, based on a series of collections from the eastern Pacific, that juveniles are between 17 and 35 mm and the adults range between 100 and 117 mm.

DISCUSSION

Although aggregations of sea urchins could be associated with reproductive activities, in the majority of cases these aggregations appear to be in response to local environmental factors or involved in social interactions (Reese 1966). Three hypotheses have been proposed to explain the benefits of these aggregations: (1) food optimization, (2) resistance to predator attack, and (3) improvement of fertilization success at spawning (see references in Campbell et al. [2001]). In the case of tropical diadematids these aggregations represent social activities and do not seem to be simple responses to environmental limitations (Pearse and Arch 1969).

Pearse and Arch (1969) studied the aggregation behavior of *Diadema setosum* in Bougainville, Papua New Guinea, and determined that they are related to protection, instead of reproduction. They suggested that when urchins are too abundant to find shelter among rocks, individuals form aggregations for protection against predators. Moreover, when a few individuals within an aggregation are disturbed, they interact with others, and the whole aggregation moves away.

Astropyga pulvinata in Bahía Culebra may be aggregating for protection against predators because they presented behavior similar to that described by Pearse and Arch (1969). However, attacks on sea urchins were not observed, and broken tests were found only rarely. Also, aggregations appear during the upwelling season, when there is no evidence of an increase of predators. Because *Astropyga* spp. are detritivores (Mortensen 1940, De Ridder and Lawrence 1982), they may be exploiting the food resources produced during the upwelling season. The aggregations are probably due to a combination of both inter-

actions (protection when abundant and food optimization). The aggregates are made up only of adult individuals, which have better protection due to their longer spines. Meanwhile, the juveniles protect themselves in caves or crevices on the rocky or reef areas.

During the upwelling season there is higher food availability, which is probably the reason the sea urchins come into shallow waters to feed. At that time of year, the thermocline is shallower (between 15 and 20 m) with a higher zooplankton abundance (Bednarski and Morales-Ramírez 2004). The sea urchins may follow the change of the thermocline position and move to shallow water to feed, descending when the thermocline sinks at the end of the upwelling. Maurer et al. (1980) reported individuals of this species on the outer part of the Gulf of Nicoya, in Costa Rica, at 35 m depth. That depth corresponded with the thermocline zone, where the temperature was close to 20°C and the PO_4^{3-} concentration was 2 μM (Epifanio et al. 1980). In Acapulco Bay (Pacific coast of Mexico), many aggregations of 5 to 30 individuals on rocky substrate were associated with the thermocline between 20 and 27 m depth (pers. obs., November 2005). This indicated that the adult behavior of *Astropyga pulvinata* is influenced by the behavior of the thermocline related to the disposition of food associated with it. A similar example of urchin aggregations to exploit food resources was observed in Japan, where *Astropyga radiata* aggregations reduced an eelgrass (*Zostera maritima*) patch (Bak and Nojima 1980), indicating migration to a food supply.

There is a possibility that these aggregations have a role in reproduction. Urchins could, for example, enhance fertilization by being aggregated during spawning. However, during the study spawning was not observed. Bauer (1976) found that *Diadema antillarum* in Florida aggregated during spawning months when sea temperatures are low, which worked as a triggering signal. In my study the focus was not on reproduction, but it should be considered in future research. Moreover, from size data (Figure 7) the observed phenomenon is not the result of local recruitment of recently metamorphosed sea

TABLE 1
Organisms Associated with *Astropyga pulvinata* at Punta
Flor, Bahía Culebra

Group	Family	Species
Crustaceans	Inachidae	<i>Stenorhynchus debilis</i>
Fishes	Serranidae	<i>Alpbeste multiguttatus</i>
		<i>Dermatolepis dermatolepis</i>
		<i>Rypticus bicolor</i>
	Grammistidae	<i>Apogon dovii</i>
		<i>Apogon pacifici</i>
	Apogonidae	Not identified
	Haemulidae	<i>Lutjanus guttatus</i>
	Lutjanidae	<i>Chaetodon humeralis</i>
	Chaetodontidae	<i>Pomacanthus zonipectus</i>
	Pomacanthidae	<i>Halichoeres dispilus</i>
	Labridae	

urchins but rather the immigration of adult individuals from elsewhere.

The diadematids have been recognized as refuges for several species of fishes, favoring the development of juvenile stages and in some cases adults and serving as biogenic structures that provide protection (Randall et al. 1964, Teytaud 1971, Hartney and Grorud 2002, Kolm and Berglund 2003). In my study, 10 species of fishes and one crab species (*Stenorhynchus debilis*) were observed associated with the *Astropyga* aggregations (Table 1). The fishes that were found most often were adults of *Rypticus bicolor*, which dig under the urchin spines, and two species of *Apogon*. The first species was observed close to the sand, under the spines of the urchin, and the apogonids were observed between the spines in high numbers. *Apogon* is commonly associated with diadematid aggregations (Kier and Grant 1965, Zann 1980, Moosleitner 2002, Kolm and Berglund 2003). Kolm and Berglund (2003) determined that densities of *Pterapogon kauderni* were positively correlated with aggregations of *Diadema setosum* in Sulawesi, indicating that the urchins formed an important habitat for the fish, which are under strong extraction pressure from the aquarium trade. Those authors concluded that these aggregations have an important conservation value for the fish because they provide a refuge. Based on the evidence from other regions of the world, the aggregations of *Astropyga pulvinata* in Bahía

Culebra act as a refuge too. This area of the country is subjected to much fish extraction for aquariums (Cortés 1996–1997, Ibarra 1996), so the urchins could have a high conservation value for several fish species in the region.

In the past few years, the local people of Bahía Culebra have seen a reduction of the populations of *Astropyga pulvinata*, which is being extracted for the aquarium trade. Consequently, it is important to continue monitoring these populations and the impact of their disappearance on other species.

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